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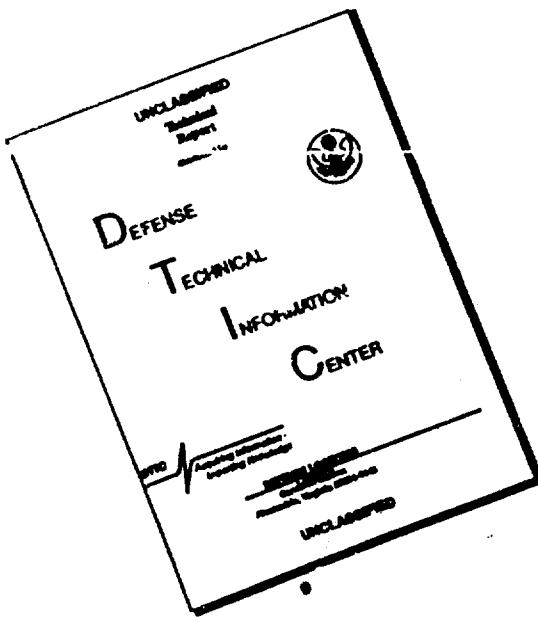
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COMPARATIVE ECOLOGY OF BLOODSUCKING DIPTERA

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III. The Significance of the Crop in the Water Balance of Horseflies (Family Tabanidae)*

1. Introduction

Under natural conditions most horseflies regularly ingest significant amounts of free liquids. Their crop (ingluvies), as in most bloodsucking Diptera, is the receptacle for these liquids and the organ controlling the gradual and rhythmic delivery of water to the stomach. In mosquitoes it prevents lethal dilution of the hemolymph and frees the insect from the need for frequently repeated intake of water. It was of interest to ascertain directly whether it played the same dual role in horseflies.

2. Experimental Method

Female horseflies of the following species were used in the experiments: Tabanus bromius L. -- 12 individuals, T. bovinus Lw. -- 88, T. arpadii Szil. -- 12, T. fulvicornis Mg. -- 14, T. cordiger Mg. -- 1, and Chrysops relictus -- 2.

The females were caught as they attacked their prey or when they flew in the laboratory window and were experimented upon so far as possible immediately after being caught. Horseflies are large

*See Z.M. Denisova, "Comparative Ecology of Bloodsucking Diptera, I. Dual Significance of the Crop in the Water Balance of Mosquitoes," Zoologicheskiy Zhurnal (Journal of Zoology), Vol 22, 1943 (literature given in the same place).

insects; therefore when injecting the liquids we did not resort to narcosis -- the insect was easily held in the necessary position. Weighing took place in a test tube. The average weight of T. arpadi is 104 mg, of T. bovinus -- 253 mg, of T. bromius -- 84 mg, and of T. fulvicornis -- 100 mg. The individual weight variation was rather appreciable, which depends on fluctuations in size of individuals and their degree of emaciation (loss of fluid, etc.).

Undamaged individuals were used as controls. The average room temperature was 21.5°C [71.7°F]. Forty-nine females in all were subjected to experimentation; 20 of them were injected with distilled water, 17 with Ringer's solution, while 12 were controls. The species makeup should have no effect on the experimental results, for the species distribution among the experiments was as uniform as possible. Account was taken of mortality every 12 hr, while in the previous experiments on mosquitoes it was taken once a day. Many phenomena take their course substantially more rapidly in horseflies than in mosquitoes. We conventionally adopted the moment of cessation of motor reaction to touch as the moment of death of the tabanids, although their hearts still kept working weakly after this. If the moment of heart stoppage is taken as the moment of death the absolute length of life in all the experiments is somewhat increased, but the relationships remain the same as given below.

3. Experimental Results

As is evident from Fig. 1, no deaths occurred in the first 12 hr among the control horseflies. Massive death in this group took place in the second half of the first day. It considerably exceeds mosquito (Anopheles maculipennis) mortality in the same period.

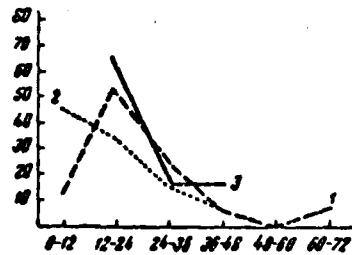


Fig. 1. Mortality Among Injected and Control Horseflies Expressed as Percentage of Initial Number of Horseflies of Each Class. Time after start of experiment laid off horizontally. 1 -- Horseflies receiving Ringer's solution, 2 -- distilled water, 3 -- controls.

Among the injected horseflies fewer deaths were observed among individuals receiving Ringer's solution (Fig. 2). During the first 12 hr of the experiment 11.8% of these individuals died. This number is close to the parallel mortality of mosquitoes on the first day of observation. In the second half of the day mortality did not exceed that among the controls. Ringer's solution cannot reduce the osmotic pressure of the hemolymph and consequently cause osmotic death. The mortality observed in these experiments apparently resulted from trauma in puncture and pressure of the liquid introduced. The latter is corroborated by

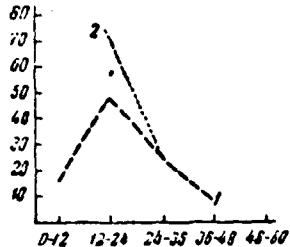


Fig. 2. Mortality in Horseflies Injected with Different Doses of Ringer's Solution. Curves plotted as in preceding figure.

1 -- Horseflies receiving more than half their body weight in solution, 2 -- receiving from 1/4 to 1/2 their body weight.

percentage of osmotic deaths also among mosquitoes on the first day.

Distilled water dilutes the hemolymph and lowers osmotic pressure. Therefore large doses of water give the highest mortality. Of the flies receiving a dose of water exceeding half their body weight 57.2 % died in 12 hr. This mortality approaches that of mosquitoes from large doses of water on the first day of the experiment. The mortality of the horseflies which on the other hand received small dose of water hardly differs from that of the Ringer's solution flies or the controls.

and amount of liquid: the largest volume of Ringer's solution (more than half the horsefly's body weight) caused the death of 16.7 % of the individuals, while smaller doses not only of Ringer's solution, but also of water did not cause death in the first 12 hr. A far greater mortality was observed among females which received distilled water (Fig. 3)

Death from injection of water in the first 12 hr was noted by us in 45 % of the cases, while a mortality of 11.8 % could be expected from trauma (as we saw above). Thus the death of 33.2 % of the individuals is to be assigned to osmotic death under experimentation. We had ascertained approximately the same per-

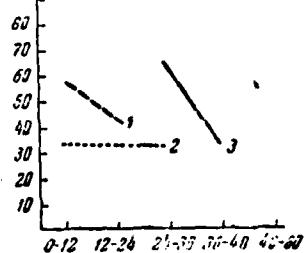


Fig. 3. Mortality in Horseflies Injected with Different Doses of Distilled Water. Curves plotted as in preceding figures.

1 -- Horseflies receiving more than 1/2 their body weight in water, 2 -- receiving from 1/4 to 1/2 their body weight, 3 -- receiving less than 1/4 of their body weight.

When observing the tabanids' behavior we found that distilled water introduced in large amounts affects the nervous system and abdominal musculature with the result that immediately after its administration abdominal movements cease, peristalsis is impaired, as well as excretion, etc. General paresis does not immediately supervene: the rapid movements of the extremities gradually become sporadic and then become weak and infrequent. This effect is irreversible and quickly brings about the insect's death. This picture is not so clearly expressed at the first moment with mosquitoes.

With small water dosages (less than 40 % of horsefly body weight) there was not such a lethal effect; all the insect's functions, including excretion, went on more or less normally, but with injection of Ringer's solution no organic necrosis occurred at any dosages.

It is thus evident that dilution of the hemolymph with a small dose of water is not fatally dangerous to horseflies. On the one hand it apparently does not exceed the limits of the natural dilutions occurring during normal consumption of water by the flies. On the other hand because of the preservation of undamaged Malpighian vessels the surplus of administered water is rapidly excreted by the flies.

Mortality on the following days of the experiment, beginning with the second day, we did not regard in the mosquitoes as associated with dilution of the hemolymph. It was chiefly caused by loss of water and, in part, by trauma. The same situation prevails with horseflies. The control flies had died off by the end of the second day. Certain signs of their fading were noted: while still alive their proboscises collapsed and gave the impression of being dried, their abdomens became transparent, and their extremities made weak, jerky movements. Later the insect ceased showing any signs of life at all. Similar signs of death in horseflies were also noted in cases of injection with Ringer's solution and small doses of distilled water.

Like the controls the horseflies injected with Ringer's solution lived in part until the end of the second day. Several individuals which had received large doses of solution outlived flies which had received small doses by 12 hr. Here is the same pattern which we observed in the mosquitoes: the more Ringer's solution administered, the longer the average lifespan of individuals which do not get drink. Unfortunately the small number of data on horseflies make it impossible to state this with confidence.

The horseflies which got Ringer's solution quickly lost moisture and in the first twenty-four hours began to consume their own reserves with an up to 12 % loss in actual body weight, while on the second day their loss of weight is almost comparable with that of the controls at 19.6 % of body weight (in the controls the reduction went to 26.7 %). The horseflies which received large (lethal) doses of water died on the first day of the experiment without having used up the water received. With small doses of water a substantial portion of the horseflies kept on living until the end of the second day. They quickly excreted the excess water: some individuals lost all the water received by injection in the very first 12 hr of the experiment (loss of actual weight of up to 0.3 %).

Subsequently excretion took its full course. By the end of the second day weight loss had reached 26.5 %. Here, in contrast to the action of Ringer's solution, a second pattern is observed: the less the amount of water administered, the weaker is its harmful effect and the longer the horseflies in the experiment survive. The horseflies which received minimum water dosages died off at the same time as the controls.

Excretion of liquid through the Malpighian vessels and anal opening in horseflies injected with Ringer's solution or small doses of water had already begun 10 to 15 min after injection. Horseflies are great dissipators of fluid: all our data indicate the rapid drop in horsefly weight, chiefly through the rapid consumption of water getting into their bodies through the ingluvies. Therefore average lifespan of the experimental horseflies did not exceed that of the controls. Loss of moisture has an even more lethal effect on horseflies than on mosquitoes: the control mosquitoes survived up to five days (without drinking), but the horseflies only two days (moreover at a somewhat lower temperature). Both the mosquitoes and the horseflies underwent the same proportional loss of initial weight in the first two days (up to 30 %), but the latter withstood this loss more poorly.

From the material it is evident that the horseflies, both those injected and the controls, die considerably faster than mosquitoes. The explanation for this is apparently that the resistance of horseflies to fluctuations in osmotic pressure of the hemolymph is less than that of mosquitoes. This may involve the fact that horseflies, active during the whole sunlit part of the day, may because of the rapidity of their flight replenish their water reserves as necessary and thus actively ensure a constant amount of water in their bodies; it may be thought that because of this their tissues are adapted to a constant osmotic pressure of the hemolymph and poorly withstand variations therein. There are, however, no data on hemolymph osmotic pressure in horseflies in the literature, and therefore the explanation given remains suppositional.

Conclusions

1. Distilled water introduced into the body cavity of the horsefly in large quantity (no less than half of body weight) lowers hemolymph osmotic pressure and causes necrosis of the organs and rapid death of a substantial number of individuals.
2. Liquid which has entered directly into the body cavity is quickly excreted by the Malpighian vessels. Horseflies with parenterally administered Ringer's solution die from loss of water at the same time as control flies (by the end of two days). In the experi-

ment the horseflies die of desiccation somewhat more rapidly than do mosquitoes and in somewhat larger percentage with the same loss of water.

3. Horseflies withstand fluctuations in osmotic pressure of the hemolymph more poorly than do mosquitoes. This is apparently associated with their vital pattern (greater mobility providing the opportunity for more frequently drinking water and the associated adaptation to more stable osmotic conditions in the internal medium).

4. The crop (ingluvies) in horseflies has, in addition to its role in double feeding, great significance in providing the organism with water. Water from the crop passes gradually into the stomach in small amounts, which eliminates the possibility of an abrupt drop in hemolymph osmotic pressure fatal to the organism and on the other hand ensures economical use of the water imbibed.